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LATE DEVONIAN (FAMENNIAN) LUNGFISHES FROM THE CATSKILL FORMATION OF PENNSYLVANIA, USA

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Abstract: Occurrences of fossil lungfishes (Dipnoi: Sarcopterygii) in the Famennian Catskill Formation of Pennsylvania are reviewed. A nearly complete dermal skull roof is assigned to a new genus and species, *Apatorhynchus opistheretmus*. Other recently discovered lungfish specimens include an incomplete postcranium similar to that of the Frasnian genus *Fleurantia*, a small parasphenoid of uncertain affinities, and isolated toothplates. Previously described dipnoan remains from the Catskill Formation include a partial skull roof of *Soederberghia groenlandica*, toothplates assigned to several species of *Dipterus*, a putative rostral or symphysial region placed in the problematic form taxon *Ganorhynchus*, and sedimentary structures interpreted as burrows. The toothplates attributed to *Dipterus* are indeterminate and are placed in open nomenclature, while the specimen identified as *Ganorhynchus* is not convincingly dipnoan. The status of the burrows remains uncertain pending the discovery of lungfish remains within these or similar structures in Catskill deposits. The distinct ichthyofaunas within the Catskill Formation and their lungfish components are briefly reviewed. Lungfishes are found in the *Holoptychius*- and *Bothriolepis*-dominated faunas common in the Catskill succession, as well as in the compositionally distinctive Red Hill assemblage. Many of the Devonian continental faunas that contain tetrapods also include long-snouted, denticle-bearing lungfishes ('rhynchodipterids', fleurantiids, or both). The composition of Late Devonian ichthyofaunas may have predictive qualities that will allow researchers to identify localities likely to produce the remains of early tetrapods.

Key words: Catskill Formation, Dipnoi, Famennian, fauna, Osteichthyes, Sarcopterygii.

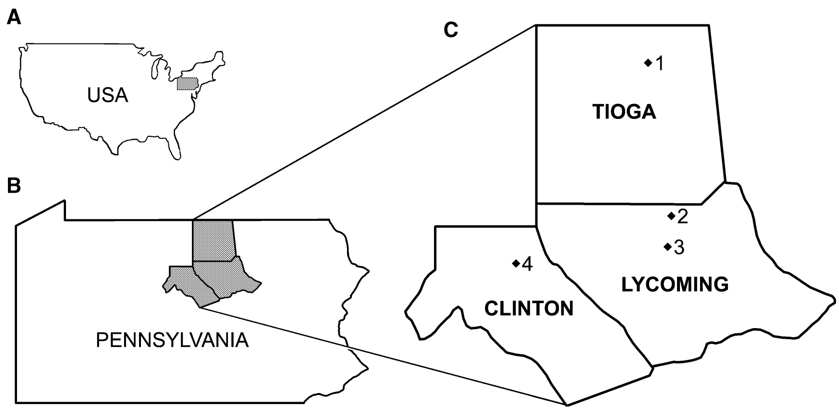
LUNGFISHES (Dipnoi: Sarcopterygii) are a common component of late Palaeozoic ichthyofaunas, particularly in nearshore marine and continental depositional environments. The Upper Devonian (Famennian) Catskill Formation has yielded sparse remains of dipnoans that co-occur with a rich vertebrate fauna that also includes porolepiform and tetrapodomorph sarcopterygians, actinopterygians, acanthodians, chondrichthyans and placoderms (Daeschler *et al.* 2003; Table 1). The sediments, flora and fauna of the Catskill Formation provide data on the development of continental ecosystems during the Late Devonian, and establish the environmental context for the evolutionary transition between 'fishes' and limbed vertebrates. Although dipnoans appear to have been important components of many of the Devonian communities that include tetrapods (Bendix-Ahlmgreen 1976; Thomson 1980; Lebedev 1992, 2004; Ahlberg 1998; Clément and Boisvert 2006), the lungfishes of the Catskill Formation have received little attention. Here we review the dipnoans of the Catskill fauna, and include the description of a new genus and species of lungfish.

MATERIAL AND METHODS

Field parties from The Academy of Natural Sciences have been surveying and collecting at road cut exposures of the Catskill Formation in Pennsylvania since 1993. Lungfish material has been encountered infrequently. The dipnoan skull roof that is described herein as a new genus and species was found on the surface of a large boulder of fine- to medium-grained sandstone that had been excavated by heavy equipment during road construction in 2001 (Locality 1; Text-fig. 1). The internal surface of the skull was exposed, with some of the dermal bones broken away revealing a natural mould of the dorsal surface. It was clear that any attempt to use chisels or a rock saw to remove the specimen would prove unsuccessful. Thus, after photographic documentation of the specimen as it was found, the remaining bone was removed mechanically and etched with hydrochloric acid, creating a detailed natural mould. The specimen was then collected as a latex peel backed by a plaster. The latex peel was later used to recreate the natural mould in silicone, from which casts

TABLE 1. Vertebrate assemblages within the Catskill Formation containing dipnoans. Lungfishes listed in bold type. Faunal lists derived from the following references: Mansfield, Daeschler and Mullison (2004); Tioga County Roadcut, Ahlberg *et al.* (2001); Powys Curve, Davis *et al.* (2004); Red Hill, Daeschler *et al.* (2003), Shubin *et al.* (2004).

Mansfield (undifferentiated Catskill)	Lycoming County Roadcut (undifferentiated Catskill)	Powys Curve (Sherman Creek Member)	Red Hill (Duncannnon Member)
Apatorhynchus	***Soederberghia***	**Gen. et sp. indet. A**	**Gen. et sp. indet. E, F**
Bothriolepis	*Bothriolepis*	*Bothrioplepis*	*Phyllolepis*
Phyllolepis			*Groenlandaspsis*
Dinichthyidae	*Sterropterygion*	Acanthodidae	*Turrisaspis*
Holoptychius		*Holoptychius*	*Gyracanthus*
Tristichopteridae		*Sauripterus*	*Ctenacanthus*
			Ageleodus
			Limnomis
			Holoptychius
			cf. *Sauripterus*
			Rhizodontidae gen. et sp. nov.
			Megalichthyidae
			cf. *Glyptopomus*
			Hyneria
			Hynerpeton
			Densignathus
			ANSP 21350



TEXT-FIG. 1. Location of field sites in north-central Pennsylvania. Important vertebrate localities marked: 1, Mansfield; 2, Lycoming County roadcut; 3, Powys Curve; 4, Red Hill.

of the skull roof could be made (Daeschler and Mullsion 2004). The boulder containing the natural mould was later consumed by road-building activities.

With the exception of the holotype of *D. fleisheri* (AMNH 5289; genus and species uncertain C), which could not be located and is presumed lost, all specimens figured in this paper were examined by one or both of us.

Anatomical nomenclature and systematic conventions. Nomenclature of lungfish cranial dermal bones follows the alphabetic-numeric scheme established by Forster-Cooper (1937), with additional considerations drawn from White (1965) and Thomson and Campbell (1971). Where appropriate, sarcopterygian homologies as inferred by Ahlberg (1991) follow in parentheses. Naming of ossifications of the axial skeleton largely follows Arratia *et al.* (2001). Descriptive terms for toothplate cusps are derived from Thomson (1965, fig. 1).

Considerable disagreement surrounds the interrelationships of early lungfishes, and with the exception of the basal position of some Early Devonian genera, a consensus remains elusive. This places the monophyly of many 'traditional' families in some doubt (e.g. Ahlberg *et al.* 2001), and we have therefore avoided assigning any of the Catskill remains to these problematic higher taxa. Our use of families is a strictly pragmatic approach to parsing early lungfish diversity into manageable, phenetically coherent units. Reference to particular lungfish families should not be taken as an endorsement of those taxa as natural groups, and we express our uncertainty by placing groups of doubtful monophyly in inverted commas.

Content of families largely corresponds to that in Cloutier and Ahlberg (1996), with the exception of 'Rhynchodipteridae', from which we exclude *Iowadipterus* and *Rhinodipterus*, and Fleurantiidae, which we limit to *Fleurantia* and *Jarvikia*. In addition, we refer to the numerous species of *Holodipterus* (Pridmore *et al.* 1994) as 'holodipterids'.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; NYSM, New York State Museum, Albany; RMS, National Museums of Scotland, Edinburgh.

Anatomical abbreviations. 3, bone 3; apl, anterior pit-line; B, B-bone; bp.af, basal plate of the anal fin; bp.df1, basal plate of the first dorsal fin; C, C-bone; D, D-bone; E, E-bone; hs, haemal spines; I, I-bone; J, J-bone; KX, bone combining characteristics of separate K- and X-bones in *Dipterus*; L_1, bone L_1; L_2, bone L_2; lep, lepidotrichia; M, M-bone; mpl, middle pit-line; ppl, posterior pit-line; pr.p, posterior process of the I-bone; r.af, radials of the anal fin; r.df2, radials of the second dorsal fin; ri, ribs; s.c.dl, attachment scar for the dorsolateral crista; s.c.m, attachment scar for the median crista; sn.d, distal supraneurals; Y_1, bone Y_1; Y_2, bone Y_2.

SYSTEMATIC PALAEONTOLOGY

OSTEICHTHYES Huxley, 1888
SARCOPTERYGII Romer, 1955
DIPNOMORPHA Ahlberg, 1991
DIPNOI Müller, 1845
Incertae familiae

Genus APATORHYNCHUS gen. nov.

Derivation of name. Greek, *apatos*, deceptive, and *rhynchos*, snout. The combination of these roots refers to the narrow C- and E-bones of this new genus that are suggestive of an elongated snout and had previously elicited comparison with 'rhynchodipterids' (Daeschler and Mullsion 2004).

Type and only known species. Apatorhynchus opistheretmus sp. nov.

Diagnosis. As for the type and only known species.

Apatorhynchus opistheretmus sp. nov.
Text-figures 2–4

v2004 ANSP 21357 Daeschler and Mullison, p. 2, figs 2, 4

Derivation of name. Greek, *opistho*, back or rear, and *eretmus*, paddle or oar. The combination of these roots refers to the elongate posterior processes of the I-bones.

Geological context. The Catskill Formation is approximately 100 m thick in the area north of Mansfield, Pennsylvania. The single lungfish specimen was found on a sandstone block that had been excavated by heavy equipment during road construction, but it undoubtedly originated from a section of about 30 m of rock within the lower half of the Catskill Formation. The presence of *Phyllolepis* at the site suggests that it dates to the Famennian Stage of the Late Devonian. This is corroborated by analysis of a palynoflorule from the site that refines the age to the Fa2b Substage (A. Traverse, pers. comm. 2004).

The sediments at the site are laterally variable, red to green-grey sandstones and red siltstones with sedimentary features such as cross-bedding, scour marks and root casts. These features suggest deposition within fluvial systems on the alluvial or delta plain of the Catskill delta complex (Sevon 1985).

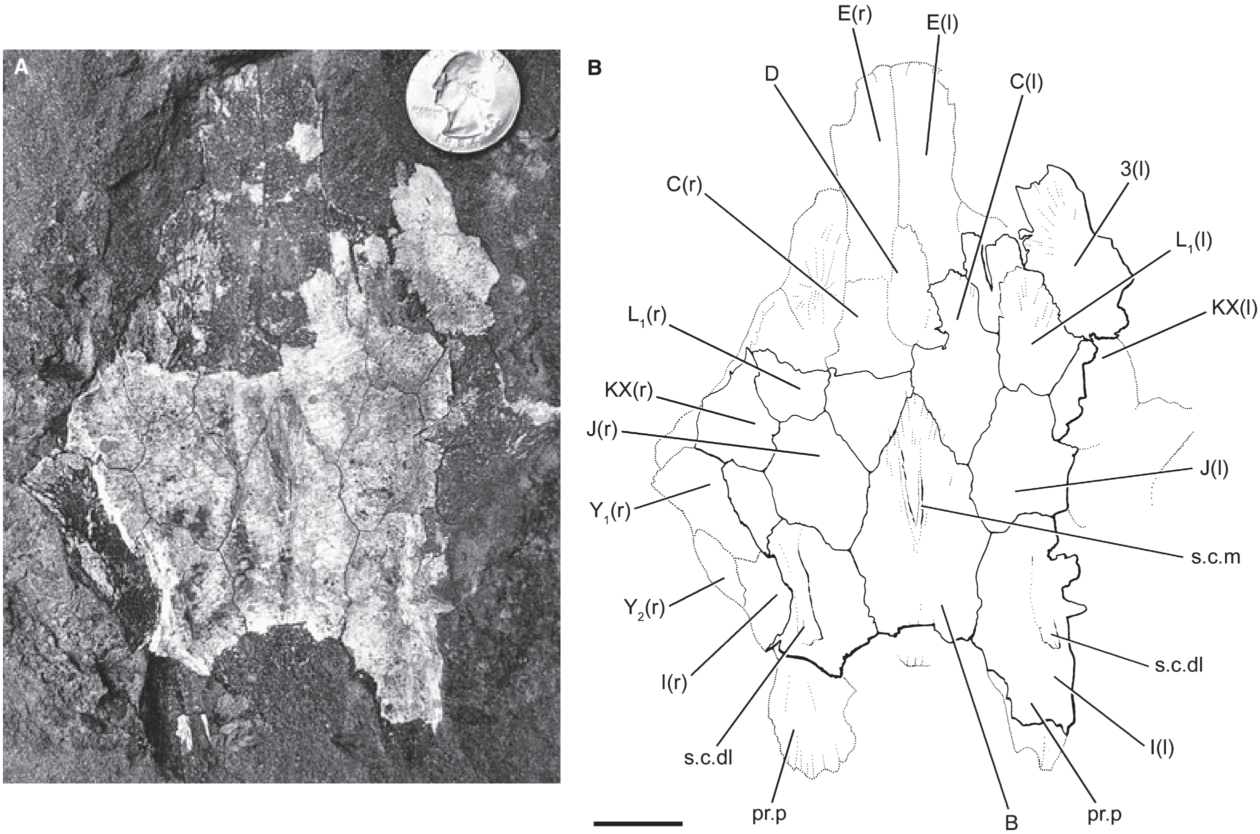
Holotype. Since the original body fossil and natural mould (Text-fig. 2) were destroyed, we designate a cast of this specimen, ANSP 21357, as the holotype (Text-fig. 3).

Type horizon and locality. Catskill Formation, undifferentiated. Late Devonian, Famennian (Fa2b). The specimen came from an outcrop on the west side of Pennsylvania Route 15 (soon to be re-named US Interstate 99) 13 km north of the town of Mansfield, Tioga County, Pennsylvania. Coordinates: N41°54·026′ W77°07·542′ (Text-fig. 1). The outcrop that yielded this specimen has been completely removed and is now the site of the Tioga Welcome Center.

Diagnosis. Cosmine absent; surface of cranial dermal bones ornamented with very fine tubercles; sutures between bones of dermal skull roof non-interdigitating with the exception of the transverse join between the C- and E-bones; I-bones with long, distally expanded posterior processes that exceed the length of the body of the bone; B-bone separates I-bones; D-bone present and enclosed by C- and E-bones; ancillary branches of supraorbital canal in C-bones; narrow, elongated E-bones that are longer than C-bones; bone 3 straddles the level of the transverse suture between the C- and E-bones; single ossification combining the characteristics of bones K and X (bone KX); multiple canal-bearing bones flanking lateral margins of C-bones anterior to KX.

Description. A majority of the dorsal surface of the dermal skull roof is known in *Apatorhynchus* (Text-fig. 3). As in most Late Devonian and all younger dipnoans, cosmine is absent. The contacts between bones are straight, and show little indication of the deeply interdigitating sutures seen in some lungfishes, most notably fleurantiids, 'holodipterids' and 'rhynchodipterids' (Graham-Smith and Westoll 1937; Lehman 1959; Miles 1977). Much of the dorsal surface of the dermal skull roof is ornamented with fine, closely spaced tubercles resembling those found in several Devonian lungfishes, including *Howidipterus* (Long 1992), *Griphognathus whitei* and 'holodipterids' (Miles 1977; Smith 1977).

None of the bones of the extrascapular series, which are represented by the median A-bone (median extrascapular) and paired



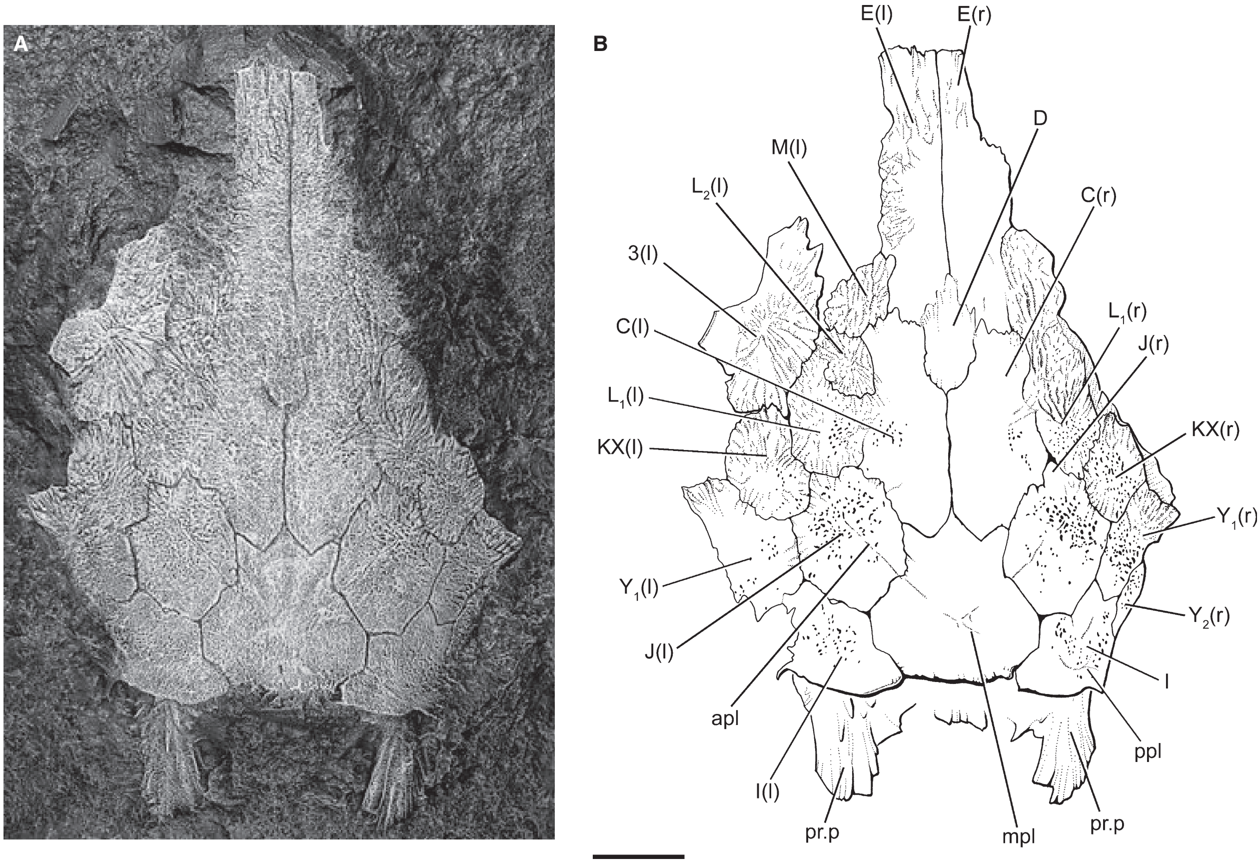
TEXT-FIG. 2. Field photograph of *Apatorhynchus opistheretmus* gen. et sp. nov. A, skull roof in visceral view. B, interpretive drawing. Scale bar represents 20 mm.

Z- and G-bones in lungfishes, is preserved in this specimen, and were presumably loosely attached to the posterior margin of the skull table. It is impossible to determine if the Z-bone was integrated into the skull roof as in most post-Devonian genera. The B-bone is the most posterior of the midline series of bones of the skull roof and resembles an anteroposteriorly compressed hexagon with a trifid anterior extension. The posterior margin of the B-bone bears a depressed flange that appears to be continuous with the posterior processes of the I-bones. The anterior and posterior pit-lines extend across the main body of the bone and converge toward its centre. The anterior pit-line continues laterally on to the J-bone (parietal) and becomes completely enclosed near the centre of that ossification. A few small pores at the right posterior corner of this bone may represent ancillary branches of the supraoccipital sensory canal (cf. *Fleurantia*; Cloutier 1996, fig. 10B), which otherwise does not appear to run through B. The absence of the occipital commissure in the B-bone indicates that it probably ran through the A-bone, as in all other Devonian lungfishes with the exception of *Jarvikia* (Lehman 1959; Campbell and Barwick 1990).

The paired C-bones are located immediately anterior to B. Each C is approximately twice as long as its maximum width. The division between the left C-bone and the more lateral ossifications of the supraorbital canal is obscure, but the different bones can be separated on the basis of surface texture and comparison with the right side of the skull. A series of pores located near the lateral margin of each C marks the position of a buried branch of the supraorbital canal, which continues laterally within the most posterior L-bone. The E-bones lie immediately anterior to the C-bones, and along with them surround the teardrop-shaped D-bone. There is no pineal foramen. The transverse suture between the C-bones and the narrower and longer E-bones is moderately interdigitated and is located at midlength of the D-bone. The surface of each E-bone is marked by ramifying grooves located along its lateral border and near its uneven anterior margin. There is no indication of any additional ossifications anterior to the E-bones.

The I-bones (postparietals) flank the B-bone, and along with it define the gently concave posterior margin of the skull roof. Each of the I-bones has a large posterior process that exceeds the length of the main body of the bone. These subdermal processes flare distally and bear longitudinal striations. The margins of the I-bone are straight where they contact other bones of the skull roof, with distinctive, wedge-shaped extensions whose apices are located at triple junctions. A series of small pores on the I-bones marks the course of the occipital commissure, while narrow grooves on the right example are interpreted as extensions of the middle and posterior pit lines. J lies anterior to I, and carries a buried sensory canal that extends posteromedially from KX and a continuation of the anterior pit line from B.

Both Y_2 (tabular) and Y_1 (supratemporal) are present in *Apatorhynchus*, and the surface of each is pitted by a series of



TEXT-FIG. 3. *Apatorhynchus opistheretmus* gen. et sp. nov., cast designated as holotype, ANSP 21357. A, photograph of a painted cast of the dorsal surface of the dermal skull roof. B, interpretive drawing. Scale bar represents 20 mm.

sensory pores that mark the course of the buried otic canal. Only the right Y_2 is preserved and much of it is obscured, but it is clear that this bone excludes the posterior half of Y_1 from the margin of the opercular embayment. Y_1 has an anteroposteriorly elongate corpus and a short lateral extension giving it an 'L'-shaped profile. Anterolaterally, Y_1 bears a flattened shelf that was presumably overlapped by bone 4 of the cheek. The bone immediately anterior to Y_1 contains the intersection of the supraorbital, infraorbital and otic canals as well as a secondary sensory canal that extends on to J. These features are located on separate K- and X-bones in most specimens of *Dipterus* (Westoll 1949, figs 2–4), the genus for which the alphabetic-numeric naming scheme was devised. The ossification in *Apatorhynchus* is identified here as KX since it combines the characteristics of these individual bones in *Dipterus*. Our choice of name is not meant to imply that this bone formed by fusion of bones K and X; an identical morphology could have also arisen through bone loss. Bone KX bears a depressed shelf laterally that is continuous with the overlap area for bone 4 found on Y_1.

The supraorbital series anterior to KX consists of several ossifications, but the boundaries between individual bones in this region are indistinct. Three separate ossifications are preserved on the left side of the specimen, while the condition on the opposite side of the skull is less clear. The naming of bones in this position is inconsistent in the literature, and there are no clear and readily justifiable criteria underlying competing nomenclatural schemes (Thomson and Campbell 1971, p. 22). We adopt the most frequently used system, and identify these elements, from posterior to anterior, as L_1 and L_2 and M. These subquadrate bones are approximately equal in size, and flank the lateral margins of C and E. Laterally, these ossifications bear a smooth, depressed strip that marks the overlap area of bone 3.

The only circumorbital ossification preserved in the specimen is bone 3. This incomplete bone extends anteriorly beyond the transverse suture between the C- and E-bones, indicating the orbit was anteriorly placed. The elongation of E-bones in this genus is therefore deceptive; they have similar proportions to those of long-snouted lungfishes (Schultze 1992*a*), but do not indicate that *Apatorhynchus* had an elongated rostrum. Bone 3 is elevated near the orbital margin, giving the supraorbital region a raised appearance. The surface of 3 is deeply striated, with a texture most similar to that of the canal-bearing L- and M-bones.

The visceral surface of the dermal skull roof is incompletely known, and the only records of its morphology are photographs of the specimen taken in the field (Text-fig. 2). Therefore, only the most conspicuous features can be described with confidence. The location of divisions between some bones in internal view differs considerably from those in external view, indicating regions of bone overlap. Unlike in dorsal view, where it appears squat, the B-bone is anteroposteriorly elongated in ventral view, underlapping the posterior portions of the C-bones, the mesial portions of the J-bones and the posteromesial areas of the I-bones.

The midline of the B-bone bears a conspicuous V-shaped scar with a posteriorly orientated apex. This structure corresponds to the attachment point of the median crista of the neurocranium, one of five endoskeletal processes that connect the braincase to the skull roof in early lungfishes (Säve-Söderbergh 1952; Miles 1977). The posterior extent of this scar cannot be precisely determined from available photographs. Each of the I-bones appears to have a thickened region near its centre, corresponding to the attachment point of the dorsolateral crista of the braincase.

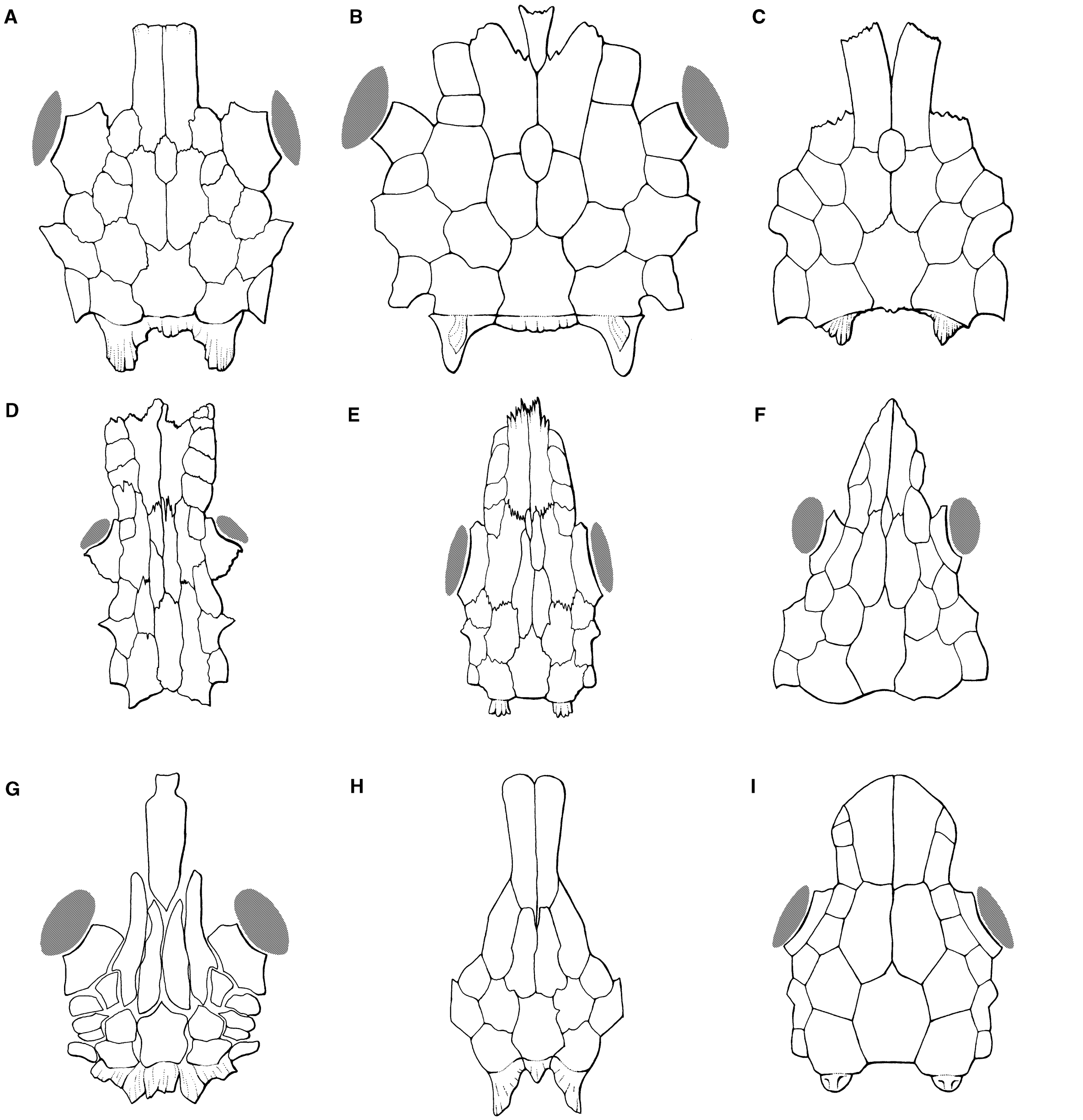
Discussion. Lungfish systematics has served as the arena for a protracted debate over methods of phylogenetic inference (Miles 1975, 1977; Campbell and Barwick 1986, 1990; Marshall 1986; Schultze and Marshall 1993; Schultze 2001), resulting in a lack of consensus among published phylogenies. Here we use the cladistic results of Schultze and Chorn (1997) and Schultze (2001) as a framework in which to interpret the systematic position of *Apatorhynchus*, as they make the most explicit claims about the distribution of characters across lungfish phylogeny.

Apatorhynchus exhibits many features that are derived relative to the most plesiomorphic lungfishes (Campbell and Barwick 1986; Schultze 2001), including anastomosis of the otic, supraorbital and infraorbital canals, the presence of well-developed E-bones, a bone that combines the characteristics of both K and X, complete separation of the I-bones by B, and the absence of cosmine. This combination of characters places *Apatorhynchus* crownward of *Dipterus*, *Adololopas*, *Rhinodipterus* and 'chirodipterids' (Schultze and Chorn 1997; Schultze 2001). Based on comparison with these proximal outgroups (*Dipterus,* White 1965; *Adololopas*, Campbell and Barwick 1998; *Rhinodipterus*, Schultze 1992*a*; 'chirodipterids', Miles 1977), *Apatorhynchus* has four characters that appear to be derived within a large radiation of Middle Devonian and younger lungfishes: a buried branch of the supraorbital canal in the C-bone, elongated E-bones, a 3 that straddles the level of the transverse suture between the C- and E-bones, and greatly elongated posterior processes of the I-bones.

A buried sensory canal within the C-bone is only seen consistently in *Andreyevichthys* (Krupina 1987, fig. 1) and the long-snouted forms *Griphognathus minutidens* (Schultze 1969, figs 10, 12) and *Fleurantia* (Cloutier 1996, fig. 10). At least one specimen of *Dipterus* (White 1965, fig. 27) has a branch of the supraorbital canal in one C-bone, but no figured skull roofs have buried canals in both. The presence of a sensory canal in C in *Apatorhynchus*, *Andreyevichthys*, *Griphognathus* and *Fleurantia*, coupled with the elongated E-bones shared by these taxa, might be taken as evidence of a close relationship between them, consistent with earlier suggestions that the new genus may be allied with 'rhynchodipterids' (Daeschler and Mullsion 2004). However, the similarities between the skull roof *Apatorhynchus* and those of 'rhynchodipterids' are superficial. With the exception of the division between the C- and E-bones, *Apatorhynchus* lacks deeply interdigitating transverse sutures of the skull roof, a derived character found in 'rhynchodipterids' as well as 'holodipterids' and fleurantiids, which may be closely related to them (Campbell and Barwick 1990; Schultze 2001). In all 'rhynchodipterids' (and indeed nearly all other Devonian lungfishes), the bulk of bone 3, and therefore much of the orbit, lies behind the anterior margin of the C-bones (Text-fig. 4D–G, I). However, bone 3 of *Apatorhynchus* straddles the transverse suture between the C- and E-bones, indicating that the orbit is anteriorly placed in this genus (Text-fig. 4A). These cranial proportions are very dissimilar from those of 'rhynchodipterids' and fleurantiids.

Bone 3 extends beyond the anterior margin of the C-bones in the basal forms *Dipnorhynchus* (Campbell *et al.* 1995, figs 3–6), *Erikia* (Chang and Wang 1995, fig. 3), *Jessenia* (Otto and Bardenheuer 1996, figs 1–2) and *Iowadipterus* (Schultze 1992*a*, fig. 10). It is probable that this arrangement represents the plesiomorphic lungfish condition. However, this character seems to represent a reversal within the derived clade containing *Apatorhynchus* based on comparison with the most proximal outgroups to this radiation (Schultze 2001), in which 3 lies behind the anterior margin of C (White 1965; Miles 1977; Schultze 1992*a*; Campbell and Barwick 1998). Among this set of lungfishes, the Devonian *Phaneropleuron* (Westoll 1949, fig. 7) and Carboniferous *Ctenodus* (Westoll 1949, fig. 9; Thomson 1965, fig. 2; Text-fig. 4B) and *Tranodis* (Schultze and Bolt 1996, fig. 2) have a relationship between bone 3 and C similar to that found in *Apatorhynchus*. The same arrangement has been inferred for the Carboniferous (Tournaisian) *Delatitia* (Long and Campbell 1985, fig. 3). Although they lack paired C-bones, other post-Devonian genera including *Conchopoma* and *Sagenodus* (Westoll 1949, fig. 8; Schultze 1975, fig. 4) also appear to have an anteriorly shifted 3 based on its position relative to the posterior margin of the E-bones. The anterior placement of the orbits relative to the division between the C- and E-bones, or relative to the posterior margin of the E-bones alone in those forms lacking paired C-bones, might therefore represent a synapomorphy placing *Apatorhynchus* crownward of many of its Late Devonian contemporaries, including 'rhynchodopterids', 'holodipterids' and fleurantiids.

The extensive posterior processes of the I-bones in *Apatorhynchus*, although derived, do not elucidate the systematic position of this genus. This character is sporadically distributed among early lungfishes, occurring in *Rhinodipterus* (Ørvig 1961, pl. 2, fig. 1; White 1962;



TEXT-FIG. 4. Comparison of dermal skull roof morphology between *Apatorhynchus opistheretmus* gen. et sp. nov. and a series of Late Devonian and Carboniferous lungfishes. The distance between the anterior margin of the E-bones and the posterior margin of B (not including the occipital flange, if present) is equal in all drawings. A, *Apatorhynchus opistheretmus* gen. et sp. nov. B, *Ctenodus* sp. (modified from Westoll 1949). C, *Delatitia breviceps* (modified from Long and Campbell 1985). D, *Soederberghia groenlandica* (modified from Lehman 1959). E, *Fleurantia denticulata* (modified from Cloutier 1996). F, *Rhinodipterus ulrichi* (modified from Schultze 1992*a*). G, *Andreyevichthys epitomus* (modified from Krupina 1987). H, *Oervigia nordica* (modified from Lehman 1959). I, *Scaumenacia curta* (modified from Cloutier 1996). Shaded regions indicate approximate placement of orbit in those species in which it is known. The circumorbital bones of *Oervigia* and *Delatitia* are unknown and they are not reconstructed here.

fig. 1), *Jarvikia arctica* (Campbell and Barwick 1990, fig. 5: the skull roof of *J. lebedevi* is incompletely known; Krupina 1999, fig. 1), and the species of *Holodipterus* (Miles 1977, fig. 122; Pridmore *et al.* 1994, fig. 78). *Oervigia*, which shares elongated E-bones with *Apatorhynchus*, also has well-developed posterior processes of the I-bones (Lehman 1959, fig. 26; Text-fig. 4H). These taxa are clearly distinct, however, as *Oervigia* is characterized by two derived features not present in *Apatorhynchus*: a single bone of the supraorbital series flanking the lateral margin of the C-bones and the absence of the D-bone.

Genus SOEDERBERGHIA Lehman, 1959

Type species. Soederberghia groenlandica from the Late Devonian (Famennian) Aina Dal Formation, 'Remigolepis Series', East Greenland.

Soederberghia groenlandica Lehman, 1959
Text-figure 5

For synonymy, see Schultze (1992*b*)

TEXT-FIG. 5. *Soederberghia groenlandica*, ANSP 21350. Scale bar represents 10 mm.

Material. A single skull roof, ANSP 20902, preserved in part and counterpart. Recovered from a road cut on the west side of Route 15 in Lycoming County, approximately 2·5 km south of the Tioga/Lycoming County line.

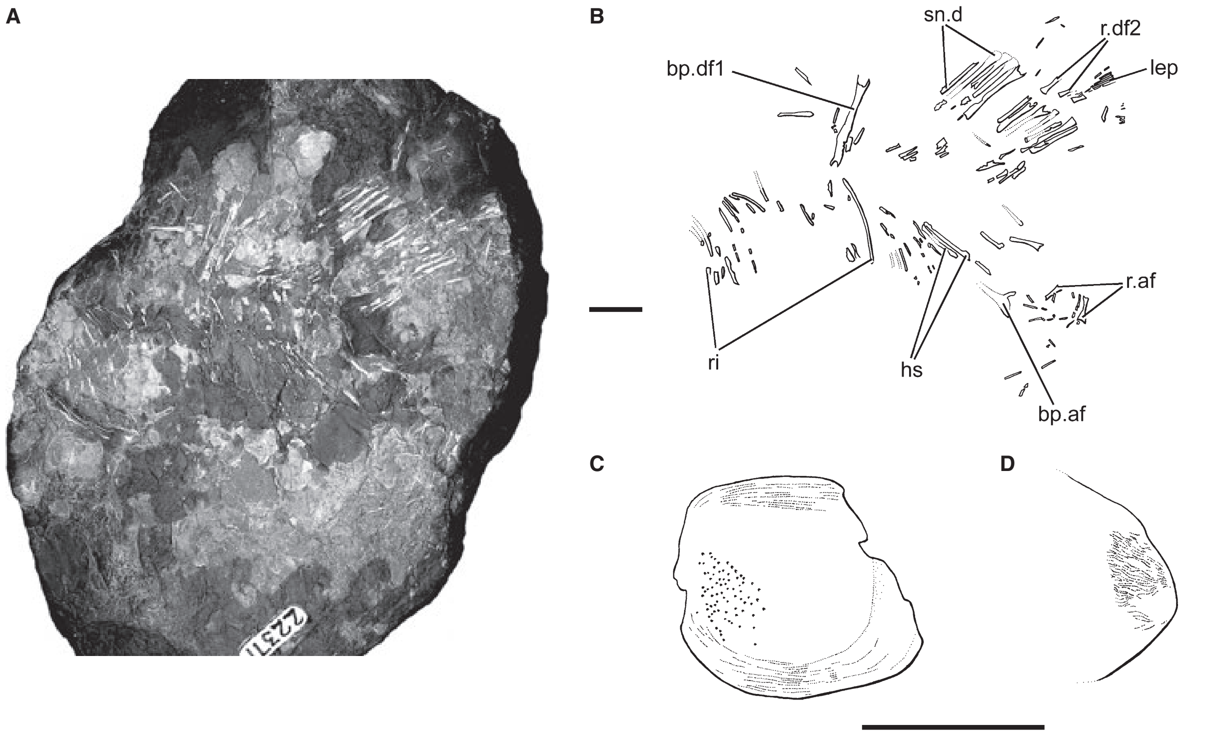
Description. For a complete description, see Ahlberg *et al.* (2001).

Remarks. Soederberghia groenlandica is a widely distributed 'rhynchodipterid' lungfish, and in addition to Pennsylvania and the type locality in East Greenland, it is also known from the Famennian (Young 1993) or late Frasnian (Young 1999) Cloghnan Shale near Forbes, New South Wales (Campbell and Bell 1982; Ahlberg *et al.* 2001). Incomplete remains attributable to this genus have been discovered in the Famennian Evieux Formation of Belgium (Clément and Boisvert 2006). *Rhynchodipterus*, which is probably closely related to *Soederberghia*, is known from similarly aged continental deposits in Scotland (Säve-Söderbergh 1937; Miles 1968). As first noted by Thomson (1980), *Soederberghia* frequently co-occurs with tetrapods (Aina Dal Formation: *Acanthostega* and *Ichthyostega*; Catskill Formation: ANSP 21350, *Densignathus*, *Hynerpeton*; Cloghnan Shale: *Metaxygnathus*; Belgium: an unnamed taxon similar to *Ichthyostega*; see 'Discussion').

Gen. et sp. indet. A
Text-figure 6

Material. A poorly preserved postcranium missing paired fins and the caudal region, ANSP 22371. Catskill Formation, Sherman Creek Member; Route 15, Powys Curve, 16 km north of Williamsport, Lycoming County. Collected in talus of locally derived rock along the side of the highway.

Description. This small specimen preserves details of the squamation and internal axial skeleton, and is recognizable as lungfish by its well-developed thoracic ribs and its proximally unsegmented lepidotrichia. The ribs are narrow and strongly curved. There is no evidence of any vertebral ossifications. Proximal supraneurals are present, but it is impossible to determine if these are compound structures that are fused to the neural arches as in some lungfishes (Arratia *et al.* 2001). Haemal spines are visible posteriorly, but it is difficult to determine their anterior extent due to poor preservation. The endoskeleton of the second dorsal fin lacks a differentiated basal plate and consists of a series of no fewer than 13 distal supraneurals that articulate with the neural spines. Some supraneurals articulate distally with dorsal radials. The second dorsal fin is long-based as in *Fleurantia* and *Scaumenacia* (Cloutier 1996; Arratia *et al.* 2001), but is not of the composite construction seen in *Pentlandia* (M. Friedman, pers. obs. of RMS 1995.4.222) and *Barwickia* (Long 1995, p. 172) that combines a well-developed basal plate and a trailing



TEXT-FIG. 6. Dipnoi genus and species uncertain A, ANSP 22371. A, incomplete postcranium with median fins. B, interpretive drawing of postcranium. C, scale in internal view. D, scale in external view. Upper scale bar for A and B, and lower scale bar for C and D both represent 10 mm.

series of supraneurals and dorsal radials. The position of the independent first dorsal fin is marked by a basal plate. This bone is poorly preserved, but it is clear that it was similar in shape to the narrow plate found in *Fleurantia* (Cloutier 1996, fig. 7) but unlike the equivalent ossification in *Dipterus*, which is comparatively robust and bears a well-developed anterior process (Ahlberg and Trewin 1995, fig. 5). A broad fragment of endoskeletal bone located near the ventral margin of the specimen is most likely to be the distal expansion of the basal plate of the anal fin. The caudal fin is not preserved.

As in most Late Devonian lungfishes, the scales are round and devoid of cosmine. The internal surface is marked by a series of concentric ridges near the margin, with small punctae present posteriorly. With the exception of the exposed field, the external surface of the scales is covered by fine radiating and concentric grooves that result in a finely denticulate texture similar to that seen in *Fleurantia* (Cloutier 1996, fig. 9E). The free field is covered with fine, subparallel ridges.

Remarks. Although the systematic affinities of this specimen cannot be determined with confidence, it is clearly not attributable to *Soederberghia*. The morphology of the postcranium is inconsistent with that genus, which retains a large basal plate in the endoskeleton of the second dorsal fin (Ahlberg *et al.* 2001). Furthermore, the Catskill specimen lacks ossified disc centra, which characterize *Soederberghia* and other 'rhynchodipterids' (Säve-Söderbergh 1937; Schultze 1969, 1970; Arratia *et al.* 2001), as well as the fleurantiid *Jarvikia* (Lehman 1959). It could belong to *Apatorhynchus*, although this would be unlikely if that genus is closely related to *Phaneropleuron* and Carboniferous lungfishes, none of which is known to retain an independent first dorsal fin.

This specimen is similar to *Fleurantia*, the only other Devonian lungfish known to combine a long-based second dorsal fin that lacks a basal plate with a first dorsal fin that retains a basal plate. All other Devonian lungfishes with long-based second dorsal fins either have no basal plates contributing to the first and second dorsal fin endoskeletons (*Phaneropleuron*, *Scaumenacia*), or retain basal plates in both (*Barwickia*, *Howidipterus*, *Pentlandia*, and an unnamed form from East Greenland; Ahlberg and Trewin 1995, fig. 12). Although a long-based second dorsal fin is derived among Devonian lungfishes, it is not unique to *Fleurantia* and the Catskill specimen, while retention of a basal plate in the endoskeleton of the first dorsal fin is the generalized sarcopterygian condition (Andrews and Westoll 1970; Ahlberg and Trewin 1995; Forey 1998). More precise taxonomic placement must await the discovery of associated cranial material.

Gen. et sp. indet. B
Text-figure 7A

v1890 *Dipterus* (*Ctenodus*) *radiatus* Newberry *nomen nudum*; Newberry, p. 119, pl. 27, fig. 33
v**1899* *Dipterus contraversus* (Newberry); Hay, p. 786
v*1908* *Dipterus contraversus* Hay; Hussakof, p. 51

Material. The holotype, AMNH 5329, is a poorly preserved toothplate from the Catskill Formation of Tioga County.

Description. Toothplate with five curved, divergent tooth ridges composed of faintly defined tubercles. Lateral ridges are more curved than those located mesially. Cosmine absent from surface of the toothplate.

Remarks. The name erected by Newberry (1890) for this taxon is preoccupied by *Dipterus radiatus* Pander, 1858, which is based on isolated toothplates from the Devonian Russian platform; Hay (1899) proposed the specific epithet *contraversus* to accommodate the Catskill form. Newberry's (1890) figure suggests that this toothplate is isolated, but the specimen is embedded in matrix, while its tooth ridges are not as clearly defined as this illustration indicates.

The only known specimen of *D. contraversus* is a badly eroded toothplate, and there is no clear evidence for a close relationship between it and the type species of *Dipterus*, *D. valenciennesi*. The attribution of this specimen and other Catskill fossils to *Dipterus* is symptomatic of nineteenth and early twentieth century taxonomic practice. As a matter of convention, *Dipterus* was applied as a stratigraphic taxon, with 'older Dipterines [classified] as belonging to the genus *Dipterus*' (Newberry 1890, p. 88). Although Newberry (1890) viewed his identifications of the Catskill toothplates as provisional pending the discovery of new material and subsequent refinement of generic diagnoses, *Dipterus* has nevertheless persisted as an accommodating taxonomic repository for isolated toothplates and other fragmentary lungfish remains, many of which are clearly not attributable to that genus (Denison 1974, p. 45). Erection of new species of *Dipterus* for isolated toothplates (e.g. Krupina 2000) seems largely unwarranted and we consider that the genus should be restricted to *D. valenciennesi*, which has been extensively described (Watson and Gill 1923; Westoll 1949; White 1965; Ahlberg and Trewin 1995) and is known from hundreds, if not thousands, of complete specimens. Given the lack of any clear synapomorphies with *D. valenciennesi*, coupled with poor preservation and a lack of diagnostic features that prevent us from reliably assigning it to another lungfish taxon, we place AMNH 5329 in open nomenclature as an indeterminate dipnoan.

Gen. et sp. indet. C
Text-figure 7B

*1897 *Ctenodus fleisheri* Newberry; Newberry, p. 302, pl. 24, fig. 25
1907 *Dipterus fleischeri* (Newberry); Eastman, p. 22, pl. 7, fig. 2
1908 *Dipterus fleisheri* (Newberry); Hussakof, p. 52
1908 *Dipterus fleischeri* (Newberry); Eastman, p. 212, pl. 2, fig. 16
1974 *Dipterus fleisheri* (Newberry); Denison, p. 41, fig. 3

Material. The holotype, AMNH 5289, is a right pterygoid toothplate from the Catskill Formation near Troy, Bradford County, Pennsylvania. The whereabouts of this specimen is uncertain; it cannot be located at AMNH. Eastman (1907) reported and figured an additional specimen (also a right pterygoid toothplate) from the Catskill Formation in Delaware County, housed in the New York State Museum (NYSM 10341) and figured by Denison (1974, fig. 3).

Description. Pterygoid toothplates with seven widely spaced, linear tooth ridges. Separate, laterally compressed cusps present along each tooth ridge. Cosmine absent from toothplates.

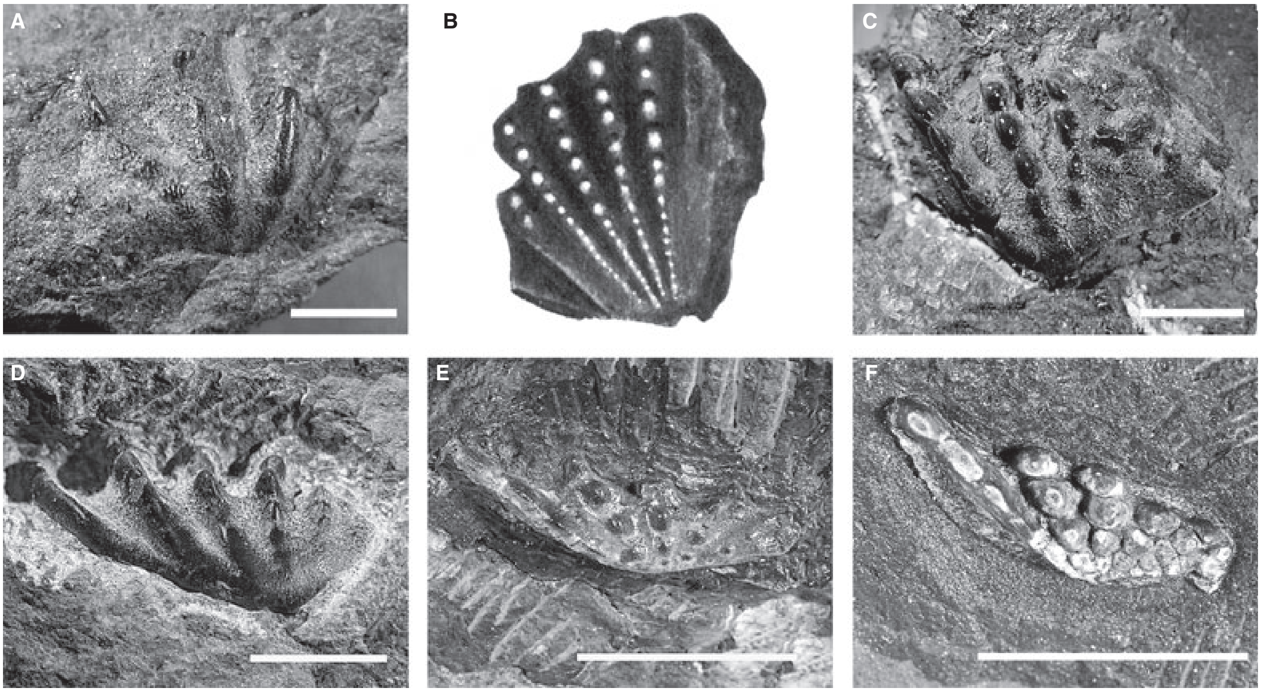
Remarks. The material attributed to *Dipterus fleisheri* differs from the type species of *Dipterus*, *D. valenciennesi*, in the number of tooth ridges (nine in *D. valenciennesi*, seven or fewer in '*D.*' *fleisheri*) and in the absence of cosmine from the Catskill form (Denison 1974). Furthermore, the spacing between the tooth rows of the Catskill species is notably wider than in *D. valenciennesi* (Denison 1974, figs 3–4). In light of these morphological discrepancies, coupled with our reservations about the placement of isolated toothplates in *Dipterus* (see above), we see no reason to retain '*D.*' *fleisheri* within this genus. We have chosen to place this specimen in open nomenclature as an indeterminate dipnoan owing to a lack of diagnostic features.

Gen. et sp. indet. D
Text-figure 7C

*v1875 *Dipterus sherwoodi* Newberry, p. 61, pl. 58, fig. 17
v1890 *Dipterus* (*Ctenodus*) *sherwoodi* Newberry; Newberry, p. 118, pl. 27, fig. 32a–b
v*1907* *Dipterus sherwoodi* Newberry; Eastman, p. 22
v*1908* *Dipterus sherwoodi* Newberry; Hussakof, p. 52
v*1908* *Dipterus sherwoodi* Newberry; Eastman, p. 212

Material. The holotype, AMNH 357, is a poorly preserved right prearticular toothplate from the Catskill Formation, Tioga County, Pennsylvania.

Description. Prearticular toothplate with a triangular dorsal surface dominated by three prominent, divergent tooth ridges



TEXT-FIG. 7. Dipnoan toothplates from the Catskill Formation. A, Dipnoi gen. et sp. indet. B; holotype of *Dipterus contraversus* (Newberry), AMNH 5329. B, Dipnoi gen. et sp. indet. C; lithograph of holotype of *Dipterus fleisheri*, AMNH 5289, from Newberry (1897) (no scale indicated). C, Dipnoi gen. et sp. indet. D; holotype of *Dipterus sherwoodi*, AMNH 357. D, Dipnoi gen. et sp. indet. E; holotype of *Dipterus angustus*, AMNH 5286. E, toothplate from the Red Hill locality similar to that of Dipnoi gen. et sp. indet. E, ANSP 21542. F, toothplate from the Red Hill locality similar to that of Dipnoi gen. et sp. indet. E, ANSP 22127. All scale bars represent 10 mm.

separated from each other by broad troughs. Each ridge is composed of a series of well-defined, laterally compressed cusps.

Remarks. Newberry (1875) described the only specimen of *D. sherwoodi* as an 'upper' (pterygoid) toothplate, but his figure captions identify it as a 'mandibular' (prearticular) plate. This specimen is embedded in matrix, and not free as Newberry's (1890) figures suggest. This toothplate differs from that of *D. valenciennesi* in having fewer tooth ridges (nine in *D. valenciennesi*, three in '*D.*' *sherwoodi*). In light of these differences and the lack of uniquely diagnostic features of the Catskill specimen, we place it in open nomenclature as an indeterminate dipnoan.

Gen. et sp. indet. E
Text-figure 7D–F

*v1897 *Ctenodus* [*Sagenodus* (Ed.)] *angustus* Newberry, p. 303
v*1908* *Sagenodus angustus* (Newberry); Hussakof, p. 53
1917 *Dipterus angustus* (Newberry); Eastman, p. 247, pl. 8

Material. The holotype, AMNH 5286, is a left pterygoid toothplate from the Catskill Formation, Troy, Bradford County. Eastman (1917) described an additional specimen housed in the National Museum of Natural History, Smithsonian Institution, but did not report on its provenance. Recently discovered toothplates from the Red Hill locality, Clinton County (ANSP 21542, 22127; Text-fig. 7F–G), appear most similar to this morphotype.

Description. Toothplate with five straight ridges. Lingual ridge elongated, extending far anteriorly. More labial ridges obliquely orientated to lingual ridge, which defines the mesial margin of the toothplate. Individual cusps may be visible on all (Eastman 1917) or some (Newberry 1897) tooth ridges, but degree of cusp development does not appear to be related to toothplate size. Cusps can be either longitudinally or laterally compressed. A raised 'heel' located at the posteromesial angle of the toothplate marks the convergence of the innermost and three outermost ridges.

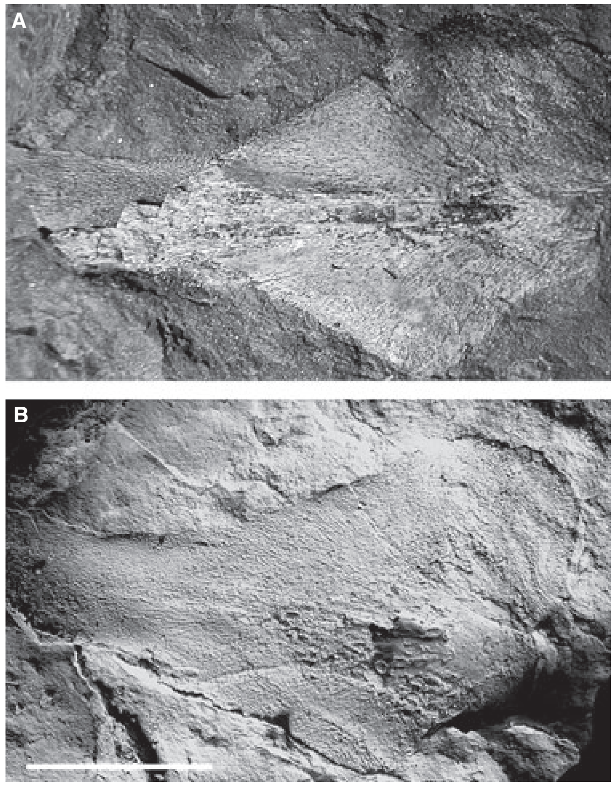
Remarks. This toothplate form has been associated with three genera, *Dipterus*, *Ctenodus* and *Sagenodus*, but there is no evidence that it can be placed within any of them. These toothplates do not correspond to those of *Dipterus* (White 1965, pl. 2; Jarvik 1967, pl. 3; Denison 1974, fig. 4) or most specimens attributed to *Ctenodus* (Watson and Gill 1923, fig. 8B), and have far fewer tooth ridges than either. However, the globose cusps (e.g. Text-fig. 7F) resemble those of the toothplate taxon '*C.*' *romeri* (Thomson 1965, pl. 3, figs G–H). The high length:width ratio of the Catskill toothplates, along with their radiating tooth ridges, are consistent with the most recent diagnosis of *Sagenodus* (Schultze and Chorn 1997), but these characters are not unique to that genus. The prominent and elongated mesial tooth ridge is found in a range of fossil dipnoans, including the Devonian genera *Andreyevichthys* (Reisz and Smith 2001, fig. 1), *Oervigia* (Lehman 1959, fig. 28), *Orlovichthys* (Krupina *et al*., figs 2, 5, 10), and *Scaumenacia* (Cloutier 1996, fig. 6), and the Carboniferous *Delatitia* (Long and Campbell 1985, fig. 4). The toothplates assigned to '*D.*' *angustus* are clearly distinct from other Catskill specimens, while their heterogeneous morphology might be evidence that they belong to several taxa. However, these specimens present too little information to permit either placement in a new genus or assignment to an established taxon. We place them in open nomenclature and provisionally regard them as indeterminate.

Gen. et sp. indet. F
Text-figure 8

Material. ANSP 22372, buccal surface of parasphenoid preserved in negative from the Catskill Formation, Red Hill site, Clinton County, Pennsylvania.

Description. The division of this isolated bone into an anterior corpus and a posterior stalk immediately distinguishes it as a lungfish parasphenoid. Preserved portions of the buccal surface are free of denticles. The ventral surface of the stalk bears a faint median depression that extends on to the corpus. A thickening, continuous with the posterior stalk, extends across the dorsal surface of the corpus, tapering and eventually terminating at the level of the lateral angles. This thickening bears a median trough. The lateral angles of the corpus are rounded.

Remarks. The absence of denticles on the buccal surface indicates that this parasphenoid cannot be attributed to *Soederberghia* (Lehman 1959), while the presence of a long, narrow stalk with a median depression is a feature common to many dipnoans (e.g. Long 1992). The rounded lateral angles of the corpus are reminiscent of most post-Devonian lungfishes, including the Carboniferous *Sagenodus* (Watson and Gill 1923, fig. 9) and *Conchopoma* (Schultze 1975, pl. 2), as well as the Permian *Gnathorhiza* (Carlson 1968, fig. 1; Berman 1976, fig. 4). A dorsal thickening with a midline trough on the corpus similar to that found in the Catskill specimen has also been noted for several lungfishes, including both *Sagenodus* (Schultze and Chorn 1997, fig. 2) and *Conchopoma* (Schultze 1975, pls 1–2). This parasphenoid cannot be positively linked to any of the toothplate morphotypes described from the Catskill Formation, and is too incomplete to be attributed to any established lungfish genus



TEXT-FIG. 8. Indeterminate lungfish parasphenoid from the Catskill Formation, Dipnoi gen. et sp. indet. F, ANSP 22372. Anterior is to the right. A, dorsal (visceral view). B, ventral (buccal) view of latex peel of acid-etched specimen dusted with ammonium chloride. Scale bar represents 10 mm.

with confidence; we leave it in open nomenclature as an indeterminate dipnoan.

DISCUSSION

Putative lungfish remains from the Catskill Formation

Cope (1892) identified a small fragment of bone as the ossified snout of a lungfish (Text-fig. 9A) and erected a new species of *Ganorhynchus*, *G. oblongus*, to contain it. We are not convinced that it belongs to a dipnoan. It lacks clear notches for the anterior nostrils, which are typically well defined on ossified lungfish rostra, and it cannot easily be interpreted as a mandibular symphysis as alternatively suggested by Cope (1892).

Ganorhynchus is a problematic form taxon applied to isolated lungfish rostra ranging in age from Middle to Late Devonian (Gross 1965; Krupina 1979). It encompasses a polyphyletic assemblage of early lungfishes (Jarvik 1980, p. 435), ranging from comparatively basal 'dipnorhynchid'-like forms such as *G. splendens* (Gross 1965, fig. 1) to *G. woodwardi* (Rosen *et al*. 1981, fig. 8), which may occupy a relatively more crownward position within dipnoan phylogeny.

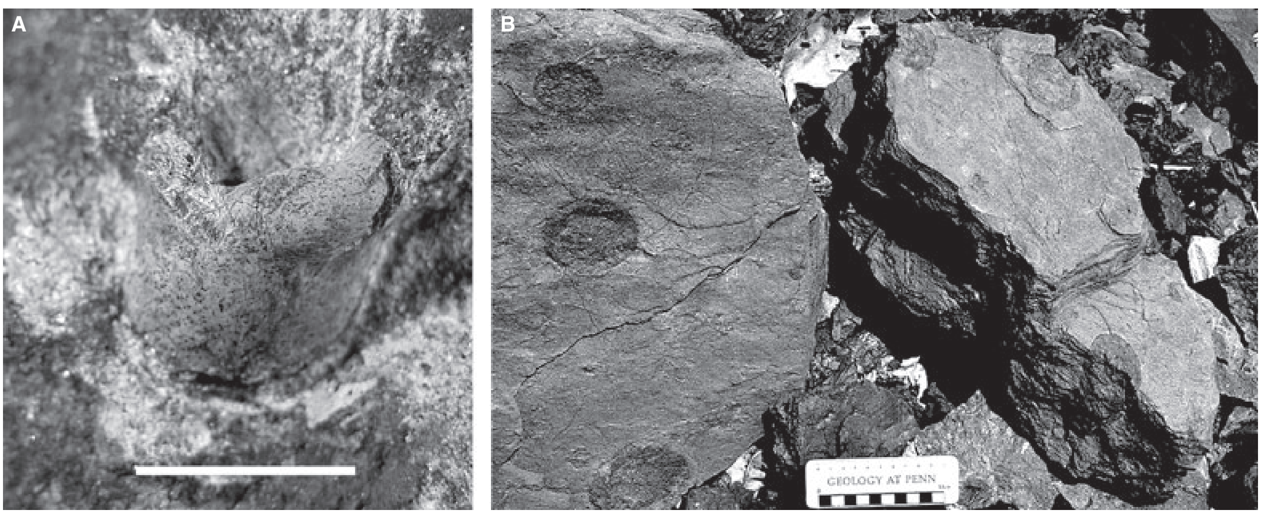
Some ichnofossils from the Catskill Formation have been interpreted as the traces of lungfishes (Text-fig. 9B). Woodrow and Fletcher (1969) identified a series of subvertical, cylindrical sedimentary structures from the Catskill Formation as dipnoan burrows. If this interpretation is correct, the Catskill burrows and roughly contemporaneous ichnofossils from Scotland and Ireland (O'Sullivan *et al.* 1986; McAllister 1992) would mark the oldest occurrence of such structures in the fossil record. However, none of these Devonian infillings has been shown to contain fossil lungfish remains, so their status as burrows must be considered doubtful (McAllister 1988, 1992). Putative dipnoan burrows from the Carboniferous of Michigan (Carroll 1965) also lack lungfish bones that would confirm such an interpretation. Permian burrows containing skeletal remains of *Gnathorhiza* (Romer and Olson 1954) are widely cited as the oldest record of lungfish burrowing. However, the incompletely described remains of a dipnoan similar to *Tranodis* have been reported from burrow-like concretions in Lower Carboniferous deposits of Kentucky (Horner and Storrs 2002), and appear to be the earliest reliable evidence of this behaviour in lungfishes.

Faunal associations within the Catskill Formation

Different sites within the Catskill Formation yield distinctive ichthyofaunas that, along with sedimentological data, provide evidence for palaeoecological heterogeneity within the Catskill Delta complex (Daeschler 1998; Daeschler *et al.* 2003; Table 1). Although collection data for many older specimens are insufficient to gauge accurately their faunal associations, the information for recently collected fossils permits a review of the ichthyofaunas of which they are a part.

A majority of localities in the Catskill Formation are dominated by the antiarch placoderm *Bothriolepis* and the porolepiform sarcopterygian *Holoptychius*, and nowhere are lungfish remains abundant. The site north of Mansfield that yielded the only specimen of *Apatorhynchus* has also produced the remains of the placoderms *Bothriolepis* and *Phyllolepis* in addition to a large arthrodire, a holoptychiid porolepiform and a tristichopterid 'osteolepiform'. Few fossils are directly associated with the Catskill specimen of *Soederberghia* (Table 1), although plates of *Bothriolepis* are present on the same block (Ahlberg *et al.* 2001). The 'osteolepiform' *Sterropterygion* was collected 1 km to the north of the *Soederberghia* locality from approximately the same stratigraphic horizon (Thomson 1972). The only articulated lungfish postcranium from the Catskill Formation (gen. et sp. indet. A) is from Powys Curve, which yields another fauna dominated by *Holoptychius* and *Bothriolepis*. In addition to these two genera, exposures at Powys Curve have also produced remains of the rhizodont *Sauripterus* (Davis *et al.* 2004), as well as an acanthodid broadly similar to *Howittacanthus* (Long 1986) and *Homalocanthus* (Gagnier 1996).

The diverse Red Hill assemblage stands in contrast to these *Holoptychius*- and *Bothriolepis*-dominated faunas and is characterized by taxa that have yet to be found elsewhere within the Catskill Formation, including groenlandaspidid placoderms, chondrichthyans, the actinopterygian *Limnomis*, and, perhaps most notably, early tetrapods (Daeschler *et al.* 1994; Daeschler 2000; Shubin *et al.* 2004; Table 1). The only lungfish remains that have



TEXT-FIG. 9. Dubious dipnoan remains from the Catskill Formation. A, indeterminate bone fragment, AMNH 2804, designated by Cope (1892) as the holotype of *Ganorhynchus oblongus*. Scale bar represents 10 mm. B, putative lungfish burrows photographed in fallen debris along Route 15, Lycoming County, Pennsylvania. Scale bar represents 10 cm.

been recovered from Red Hill are an incomplete parasphenoid (gen. et sp. indet. F) and several isolated toothplates (gen. et sp. indet. E).

Lungfishes, tetrapods, and the assembly of continental ecosystems

Lungfishes often co-occur with tetrapods in Late Devonian deposits (Lebedev 2004), while particular lungfish groups appear to be linked to fluvial depositional environments inhabited by some early tetrapods. While toothplated dipnoans were ubiquitous in both freshwater and marine environments in the latest Devonian (Janvier 1996), long-snouted, denticle-bearing forms appeared to be tied to continental ecosystems during the same interval. The oldest lungfishes of this habitus are clearly marine (the early Frasnian *Griphognathus*; Campbell and Barwick 1988), but whether the shift to continental environments from the late Frasnian onward marks an important ecological transition within a coherent clade of long-snouted dipnoans or instead points to an independent radiation of freshwater taxa similar to, but not descended from, these marine forms remains uncertain (Ahlberg *et al.* 2001). What is clear, however, is that lungfishes of this morphotype are often found in fluviatile formations that yield early tetrapods. Thomson (1980) first made note of this trend based on the co-occurrence of *Soederberghia* with *Acanthostega* and *Ichthyostega* in East Greenland (Bendix-Ahlmgreen 1976) and with *Metaxygnathus* (Campbell and Bell 1977, 1982) in New South Wales, Australia, but *Soederberghia* or other long-snouted forms have subsequently been recovered with tetrapods in additional continental deposits. A yet undescribed long-snouted lungfish is known from the Frasnian Scaat Craig beds of Scotland, which yield the remains of *Elginerpeton* (Ahlberg 1998). *Soederberghia* and the tetrapods *Hynerpeton*, *Densignathus* and ANSP 21350 (Daeschler *et al.* 1994; Daeschler 2000; Shubin *et al.* 2004) are known from different localities within the Catskill Formation (Table 1). The Famennian Evieux Formation of Belgium has produced an *Ichthyostega*-like tetrapod (Clément *et al.* 2004) and remains suggestive of *Jarvikia* and *Soederberghia* (Clément and Boisvert 2006). The only continental locality that yields Devonian tetrapods but no 'rhynchodopterid' lungfishes is the Famennian Zhongning Formation of China, from which dipnoan remains have yet to be reported (Zhu *et al.* 2002; Lebedev 2004).

In contrast to Devonian tetrapod sites dominated by freshwater deposition, those with a strong marine influence do not yield 'rhynchodipterids'. No denticle-bearing lungfishes are known from the same Frasnian beds as *Obruchevichthys*, a close relative of *Elginerpeton* (Ahlberg 1995), although toothplates have been found in these Latvian deposits (H. Blom, pers. comm. 2004). Only the remains of toothplate-bearing lungfishes similar to *Orlovichthys* have been recovered with *Ventastega* in the Famennian Ketleri Formation of Latvia (Ahlberg *et al.* 1994), while the unusual toothplated form *Andreyevichthys* is the only dipnoan found with *Tulerpeton* in the Famennian Andreyevka-2 locality in Russia (Lebedev 1992). Toothplates and dermal bones assigned to *Conchodus*, *Dipterus* and *Holodipterus* are found in the Famennian deposits of the Gornostayevka quarry along with remains of the tetrapod *Jakubsonia* (Lebedev 2004). Each of these localities has been interpreted as either nearshore (Ketleri, Gornostayevka quarry, Lebedev 2004; Ogre Beds, H. Blom, pers. comm. 2004) or fully marine (Andreyevka-2, Lebedev 1992).

Although tetrapods are members of faunas that lack long-snouted lungfishes, the consistent association between these two groups in continental settings might permit researchers to identify deposits likely to yield early tetrapods based on the character of the lungfish fauna. The Famennian Rosebrae Beds of Scotland are a notable example. These continental deposits (Peacock *et al.* 1968) have produced remains of the long-snouted lungfish *Rhynchodipterus* in addition to the tooth-plated genera *Phaneropleuron* and *Conchodus*, as well as porolepiforms, 'osteolepiforms', and phyllolepid and bothriolepid placoderms (Miles 1968). This fauna is similar to that of many tetrapod-bearing localities, but the Rosebrae beds have not yet yielded the remains of tetrapods. These and other deposits that bear similar lungfish faunas may be promising field sites for future collecting intended to illuminate the phylogenetic and environmental context of the fish-tetrapod transition.

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